

Fire-Free Hominin Strategies for Coping with Cool Winter Temperatures in North-Western Europe from Before 800,000 to Circa 400,000 Years Ago

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ABSTRACT

There is no consensus on the chronology of fire use, with suggestions ranging from earliest use by *Homo erectus* 1.8 mya to relatively recent Anatomically Modern Humans. While it is widely agreed that fire would have been of great assistance in moving into areas with a temperate climate, early sites from middle latitudes across Eurasia lack convincing evidence for fire use before about 400,000 years ago. It is not clear whether this represents a real pattern, or a limitation to past research methods and survival. Establishing a firm chronology for the use of fire requires refined interpretation of fire residues at early sites. An alternative approach, taking the pattern (provisionally) as real, is to investigate how hominins could have solved important survival problems at middle latitudes without using fire. This article addresses strategies for thermoregulation in the absence of fire in conditions experienced by hominins in north-west Europe before 400,000 years ago. Four main hypotheses are proposed, involving strategies based primarily on 1) winter fur and subcutaneous fat, 2) hibernation, 3) enhanced heat production, and 4) a combination of cultural insulation particularly clothing and insulative baby carriers with enhanced heat production. Given the trade-offs of these strategies, I will consider their plausibility for the early occupants of Europe, and discuss how the most plausible strategies could be detected in future research.

INTRODUCTION

Chronologies for the use of fire diverge widely, with suggestions varying from *Homo erectus* 1.8 mya to relatively recent Anatomically Modern Humans (Sandgathe et al. 2011; Wrangham et al. 1999). For hominins moving into more seasonal, temperate environments, fire would have had many benefits, and it has long been seen as an important factor in hominin range expansion. The archaeological evidence for fire use in relation to dispersal into cooler regions has been reviewed in detail elsewhere (Attwell et al. 2015; Gowlett 2006, 2016; MacDonald 2017; Roebroeks and Villa 2011a; Sandgathe and Berna 2017). Briefly, by the end of the Early Pleistocene (0.78 mya) stone tools and fossils document hominin presence across much of Eurasia up to 40° north, and similar evidence from north-west Europe is almost as old (Carbonell et al. 2008; Dennell 2013; Ferrer et al. 2011; Gabunia et al. 2000; Parfitt et al. 2005, 2010). In Europe, archaeological traces of anthropogenic fire are absent from the earliest sites, and become increasingly frequent from about 300,000 to 400,000 years ago (Roebroeks and Villa 2011a). In the Levant, frequencies of burnt flints and evidence for repeated use of hearths from a number of long cave sequences suggest that this is part of a wider phenomenon (Karkanas et al. 2007; Shahack-Gross et al. 2014; Shimelmitz et al. 2014). At the open air site of Gesher Benot Ya'aqov, clusters of heated stone microartifacts and small plant materials, present in multiple levels, are inter-

preted as indicating regular use of fire considerably earlier, c. 780 kya (Alpersen-Afil 2008; Alpersen-Afil and Goren-Inbar 2010; Alpersen-Afil et al. 2007, 2017; Goren-Inbar et al. 2004). Currently this remains a strikingly isolated case, contrasting with the greater frequency of evidence from Europe and the Levant after about 450–350 kya. Nevertheless, fire evidence is scarce or absent in cold phases at two Late Pleistocene cave sites in France, Pech de l'Azé IV and Roc de Marsal, and, based on this, Sandgathe and colleagues (Dibble et al. 2017, 2018; Sandgathe et al. 2011) argue that Neandertals could only exploit natural fires. However, rich evidence for Neandertal fire use does occur in full glacial conditions at a number of other sites in France (Roebroeks and Villa 2011b; Sorensen 2017). In addition, the use of Middle Paleolithic tools as fire starters has been identified through microwear analysis and experimentation (Rots 2015; Sorensen and Claud 2016; Sorensen and Rots 2014). The meaning of the gap between dispersal into more temperate, seasonal environments and the appearance of more frequent, convincing evidence for fire use c. 300,000 to 400,000 years ago is not yet clear. Have we simply failed to recover the fragile evidence for fire use in older deposits, or to account for differences in behavior affecting the location or nature of traces of fire? Or do we, as a number of authors have concluded, need to consider the possibility that hominins occupied more seasonal, temperate environments without the benefits of regular access to fire (Gowlett

TABLE 1. RANGE ESTIMATES AND INDICATOR SPECIES FOR WINTER TEMPERATURES FROM NORTH-WEST EUROPEAN SITES MORE THAN 400,000 YEARS OLD.*

Site	Stratigraphic Level	MIS	MWT (°C)	Indicator Species
HSB 3	E	>13/ 17	-3 to 0	-
Pakefield	Paiv, c	≥15	-	<i>Hippopotamus</i>
Pakefield	PaB, d	≥15	-	<i>Hippopotamus</i> , <i>Salvinia natans</i>
Pakefield	PaCii, g	≥15	-6 to 4	<i>Hippopotamus</i> , <i>Trapa natans</i> , <i>S. natans</i>
HSB 1	Brown mud	15/13	-11 to -3	-
Boxgrove	Unit 4c Slindon Silts Mbr	13	-4 to 4	-
High Lodge	C1	13?	-4 to 1	-
Mauer	-	15	-	<i>Hippopotamus</i>

*Coope (2006), Holmes et al. (2010), Parfitt et al. (2010), Sinka (1993), Wagner (2010).

(MIS: Marine Isotope Stage; MWT: mean winter temperature; HSB: Happisburgh)

2006; Rolland 1998)? Does this represent a real pattern, documenting a shift in the nature of hominin interaction with fire after 400,000 years ago, perhaps involving maintenance or manufacture (Sandgathe 2017)? The primary approach to this problem is to refine the interpretation of fire evidence, and develop other innovative proxies for fire use (Aarts et al. 2016; Goldberg et al. 2017; Reidsma et al. 2016).

An alternative approach is to develop and evaluate hypotheses about strategies for survival in which fire played a limited role. Perhaps the most important challenges for survival in the region of Europe are preparing uncooked fat and meat, maintaining warmth during winter, particularly during phases of climatic deterioration, and avoiding predators (Gowlett and Wrangham 2013). Identifying plausible strategies for dealing with these challenges could yield insights into the cultural and biological adaptations of the early occupants of Europe, and provide support for the view that the gap between evidence for dispersal and fire in middle latitudes represents a real pattern. Alternatively, if no such strategies can be identified, it is more likely that we are missing early evidence for fire use. Speth (2017) has argued that fermentation of meat, fat, and fish could have provided many of the benefits of cooking, as well as a means of storing food. In addition, differences in Neandertal gut anatomy have been suggested which might have made it possible to survive on a raw, high protein diet (Ben-Dor et al. 2016). If they can be applied to the early occupants of Europe, these suggestions help to explain how hominins could have met their nutritional needs without use of fire to cook food. This paper therefore focuses on strategies for the second challenge to survival, thermoregulation.

Surprisingly, given our widespread distribution, humans are vulnerable to cold. The human body initiates regulatory changes in metabolic heat production to maintain its core body temperature at the warm ambient temperature of 29.2°C (Kingma et al. 2014). Unclothed humans begin to feel uncomfortable at yet milder temperatures. High humidity, i.e., rainfall, further increases the rate

at which the body loses heat to the environment, as does high wind speed. A deviation of a few degrees from the normal core body temperature is enough to trigger uncontrolled hypothermia, and if this persists death can follow (Jessen 2001). The temperature at which this is likely to occur is difficult to determine; a safe limit for humans who are accustomed to clothing may be -1°C (Gilligan 2007).

This article focuses on the geographical region of north-western Europe, where hominins would have encountered the most challenging winter conditions, and on the period preceding 400,000 years ago, that is, prior to the strong increase in fire proxies at archaeological sites in Europe and the Levant. From the earliest occupation of north-west Europe (more than 800,000 years ago) to 400,000 years ago, multiple glacial-interglacial cycles occurred, and glaciations became increasingly long and severe (Head and Gibbard 2005). This article addresses the parts of the cycles in which hominins are likely to have been present in north-west Europe, which include warm interglacial conditions and also (particularly after c. 500,000 years ago) the relatively cool periods before and after full interglacial conditions were established. The climatic conditions to which hominins are likely to have been exposed in this period can be assessed in more depth based on paleo-environmental reconstructions from sites with archaeology or hominin fossils in close to primary context. This evidence has been reviewed in detail elsewhere (Ashton and Lewis 2012; Hosfield 2011; Roebroeks et al. 1992) and will only be discussed briefly here. Quantitative estimates of winter air temperatures from UK sites mostly overlap between -3 and 0 °C (Table 1) (Coope 2006; Holmes et al. 2010; Parfitt et al. 2010; Sinka 1993). This range is not altered by exclusion of High Lodge based on dating arguments (Gibbard et al. 2009). The presence of frost-sensitive species at a number of sites suggests that temperatures did not drop far below freezing for long (Parfitt et al. 2005; Wagner et al. 2010). On the other hand, the approach used to derive these estimates seems to underestimate winter temperatures (Coope 1977; White and Pettitt 2011). At several sites, molluscs, pedology, and

isotope geochemistry suggest that winter rainfall was higher than present during a number of oceanic interglacials (Candy et al. 2006; Preece et al. 2006). During the late part of the study period there is also evidence for hominin presence at sites associated with steppic fauna and pollen, and geologically attributed to the climatic deterioration both at the beginning and end of interglacial climate phases, when air temperatures cooled and winds became stronger (Antoine and Tuffreau 1993; Holman and van Kolfschoten 2011; Roberts and Parfitt 1999). Taking the tendency to underestimate temperatures into account, and the fact that estimates are not available from the younger sites and levels belonging to the coolest climatic phases, hominins faced winter temperatures ranging from mostly above freezing, to at least -4°C and probably lower, which may often have felt yet cooler due to wind or rain.

Four main hypotheses of ‘fire-free’ strategies for keeping warm in such conditions of mild cold are identified for the early occupants of Europe:

1. winter fur and subcutaneous fat,
2. hibernation,
3. physiological defenses including muscle insulation and enhanced heat production, and,
4. a combination of such physiological defenses with simple cultural insulation especially clothing and insulative infant carriers.

These hypotheses are based on the literature on survival strategies of Early and Middle Pleistocene hominins (Gilligan 2017; Hosfield 2016) and Neandertal strategies for coping with more severe cold (Stegmann et al. 2002), as well as cold adaptations by medium-sized homeotherms (Jessen 2001). Given the gaps in our knowledge of the biology of the early occupants of Europe, a comparison with other mammals is considered relevant. In the following, I will outline the thermal benefits of these strategies and identify the key trade-offs based on the relevant comparative literature. I will then consider the plausibility of these strategies for the early occupants of Europe, given the trade-offs.

WINTER FUR AND SUBCUTANEOUS FAT

The following section focuses on northern primates and medium sized mammals living in similar conditions to hominins, particularly species that were present at the same locations, listed in Table 2. Reindeer are also discussed, because there is a lot of information about the cold adaptations of this species, and they were exploited by hominins within the relevant time period at the southern French site of Caune de l’Arago.

The timing of hair loss in the human lineage is unknown, with estimates based on human and lice DNA ranging from 3 to 4 million to 240,000 years ago (reviewed in Gilligan 2010). Evolutionary hypotheses about human hair loss focus on the benefits of greater capacity for heat dumping for hominins who were increasingly efficient at bipedal locomotion and occupying ever more open environments (Lieberman 2015; Wheeler 1992). According to a recent modeling study, the considerable costs of heat loss

during the night are likely to have prevented fur loss for australopithecines (Dávid-Barrett and Dunbar 2016). It is more plausible that loss of fur formed part of a suite of adaptations in *Homo* around 2 mya allowing greater mobility in more open, hotter habitats at lower altitudes (Dávid-Barrett and Dunbar 2016). It is likely that the earliest occupants of Europe lacked fur; the hypothesis discussed here therefore implies a return of dense hair under selection in cooler conditions. A possible parallel for the development of insulating fur as a novel adaptation in a lineage may be provided by the woolly mammoth (Roca et al. 2009).

Fur keeps a shell of trapped air around the body, the insulating value of which depends on its thickness (Jessen 2001: 48). If they get enough to eat, larger mammals rarely need to increase heat production to maintain body temperature (Hart et al. 1961; Jessen 2001). A thick winter coat can substantially reduce the lower critical temperature (LCT), the temperature below which an organism increases heat production to maintain core temperatures; the LCT for reindeer is 2°C in summer and -30°C in winter (Jessen 2001; Scholander et al. 1950). Japanese macaques benefit from thick winter fur, which is longer and denser in areas with colder January temperatures, suggesting that this is an adaptation to cool climates (Hamada and Yamamoto 2010; Inagaki 1985; Inagaki and Hamada 1985; Inagaki and Nigi 1988). Japanese macaques accustomed to cold could cope with exposure to temperatures of -1.4°C without any increased heat production (Hori et al. 1977).

There are a number of reasons to expect that hominin fur would be less dense than that of macaques and non-primates (although it could be equally long), and hence insulate less well. Human hair density may scale relative to body size as part of a primate trend (with larger primates having less dense fur), although this has yet to be confirmed (Lieberman 2015). Primate hair is less dense compared with other mammals (Sandel 2013). Nevertheless, based on calculations by Aiello and Wheeler (2003) for Neandertals, adapted to the body form of the hominins from Sima de los Huesos (Arsuaga et al. 2015; Ruff 2010), relatively dispersed body hair providing 1 clo (a unit measuring the thermal resistance of clothing) of insulation would have removed any risk of hypothermia for hominins in winter (Table 3). Maintaining a comfortable body temperature would still have demanded extra energy for heat production, depending on where temperatures fell within the estimated range.

In these mammals, fur combines with subcutaneous fat to insulate the body core from its environment; the latter provides less insulation for thickness and is less important but has the benefit of quickly providing more or less insulation as needed (Jessen 2001: 47). In keeping with the lesser importance of subcutaneous fat for insulation, wild Japanese macaques tolerated mild cold despite being lean (Hori et al. 1977 cited in Stegman et al. 2002).

The calculations discussed above are based on the assumption that the early occupants of Europe had a similar thickness of subcutaneous fat to modern humans. A large increase in subcutaneous fat thickness in winter would

TABLE 2. LARGE MAMMAL SPECIES PRESENT AT NORTH-WEST EUROPEAN SITES MORE THAN 400,000 YEARS OLD.*

	HSB3	Pakefield	Boxgrove	Kaerlich G	Miesenheim	Mauer
Cervidae						
<i>Megaloceros verticornis</i> (verticornis deer)		X	X	X		
<i>Megaloceros savini</i> (Savin's giant deer)		X				
<i>Megaloceros dawkinsi</i> (Dawkin's giant deer)		X	X			
<i>Cervalces latifrons</i> (broad-fronted moose)	X		(X)	X		X
<i>Cervus elaphus</i> (red deer)	X	X	X	X	X	X
<i>Dama dama</i> (fallow deer)		X	X			
<i>Capreolus capreolus</i> (roe deer)			X		X	X
Bovidae						
<i>Bison schoetensacki</i> /B. <i>priscus</i> (bison)		X	X			X
Suina						
<i>Hippopotamus amphibius</i> (hippopotamus)		X				X
<i>Sus scrofa</i> (wild boar)		X				X
Rhinocerotidae						
<i>Stephanorhinus hundsheimensis</i> (steppe rhino)		X		X	X	X
<i>S. kirchbergensis</i> (Merck's rhinoceros)			X			X
Equidae						
<i>Equus ferus</i> (wild horse)			X			
<i>Equus</i> sp. (large)				X		
<i>Equus suessenbornensis</i>	X					
<i>Equus mosbachensis</i>						X
<i>E. altidens/hydruntinus</i> (small ass-like horse)		X				
Proboscidea						
<i>Palaeoloxodon antiquus</i> (straight-tusked elephant)		X	(X)			X
<i>Mammuthus trogontherii</i> (mammoth-steppe)		X	(X)		X	
<i>Mammuthus meridionalis</i> (southern mammoth)	X					
Carnivora						
<i>Homotherium</i> sp. (saber-toothed cat)		X				
<i>Homotherium latidens</i>						X
<i>Panthera leo</i> (lion)		X		X	X	X
<i>Panthera pardus sickenberghii</i> (leopard)						X
<i>Canis lupus</i> (wolf)		X			X	X
<i>Crocuta crocuta</i> (spotted hyaena)		X				
<i>Ursus</i> sp.		X				
<i>Ursus deningeri</i> (Deninger's bear)					X	X
<i>Ursus thibetanus</i>						X

*Data from Bradshaw et al. (2003), Parfitt et al. (2005), Stuart and Lister (2001), Wagner et al. (2010), and van Kolfschoten and Turner (1996). (HSB3: Happisburgh 3)

TABLE 3. ESTIMATED LOWER CRITICAL AND MINIMUM SUSTAINABLE TEMPERATURE*
(BM=body mass; BMR=basal metabolic rate, SA=surface area, LCT=lower critical temperature,
MST=minimum sustainable temperature SH=Sima de los Huesos).[†]

	BM (kg)	Stature (cm)	BMR (w)	SA (m ²)	LCT1** (°C)	MST1** (°C)	LCT2** (°C)	MST2** (°C)
Neandertal	80.8	167	91.63	1.90	27.3	8.0	19.9	-14.4
<i>Homo sapiens</i>	70.0	177	82.28	1.86	28.2	10.5	21.3	-10.1
SH	76.1	170	87.60	1.87	27.6	8.9	20.4	-12.9

*Following Aiello and Wheeler (2003).

**Estimates with no additional heat production or insulation.

[†]Body mass from Ruff (2010); stature from Carretero et al. (2012); all male.

^{††}Estimates with light fur affording 1 clo of insulation.

have had a number of disadvantages (adding to the energetic costs of walking, depletion throughout the winter) (Aiello and Wheeler 2003; Churchill 2014). However, based on comparison with close relatives, we also need to consider the possibility that the early occupants of Europe had a relatively thin layer of subcutaneous fat. Humans, particularly females, have relatively large fat deposits, while chimpanzees and bonobos are very lean (Zihlman and Bolter 2015). The development of large fat stores in the human lineage may be linked to bipedalism and expensive infants, suggesting that this preceded colonization of middle latitudes, but the exact timing is unknown (Zihlman and Bolter 2015). Further information is needed before it is possible to discuss the evolutionary constraints on subcutaneous fat insulation in hominins in this period.

To assess the plausibility of this strategy for hominins, we need to look at the evidence for trade-offs in other mammals. During summer and autumn, energy is allocated by mid-latitude mammals to growing a winter coat and laying down fat and this may trade off with other important activities for which energy is needed. The energetic costs of growing a winter coat are small, while fattening is more expensive (2% and up to 17% of daily summer energy costs respectively for caribou, with lower costs likely for animals living in more temperate conditions) (Boertje 1985). Relatively abundant and diverse food resources would have been available in north-west Europe during the summer and autumn, making it relatively easy for hominins to obtain the necessary macronutrients, and trade-offs between time spent foraging and other (technological, social, reproductive) activities are also likely not to have been too severe. These energetic investments can save energy in winter—roe deer have *lower* food requirements and metabolic rate when there is snow cover, because they are warm enough and put less effort into foraging (Danilkin 1996). However, additional insulative fat adds to winter transport costs (a 10kg increase in weight in caribou forms about 10% of winter daily energy requirements) (Boertje 1985).

During exercise or in hot weather, fur reduces the efficiency of heat loss by sweating (Lieberman 2015), and also non-evaporative heat loss (Wheeler 1991). This increases

demands for drinking water and lowers the temperatures at which it is possible to remain active. However, the thermoregulatory disadvantages of fur for keeping cool are less relevant at the cooler temperatures which occurred in Europe (Wheeler 1991). Terrestrial mammals living in colder regions can lose heat from thinly furred regions and through respiration (Jessen 2001: 54), and even reindeer show little sign of heat stress in summer (Iver et al. 2002).

A number of other characteristics could play a role in the thermoregulation of furry northern primates and medium sized mammals living in similar conditions to hominins. One of these is brown adipose tissue (BAT), a fat cell which transfers energy from food and energy stores into heat, using well-described mechanisms (Devlin 2015; van Marken Lichtenbelt 2012). Macaques can produce large amounts of additional heat in cold conditions following acclimatization and perhaps also as a result of developmental exposure and genetic adaptation (reviewed in Steegmann et al. 2002). Fat cells consistent with BAT have been reported in adult and foetal *Macaca mulatta* as well as *Sciureus sciureus* (Devlin 2015). The extent to which BAT plays a role in other mammals with a larger body size is not well known (Cannon and Nedergaard 2004). It would be interesting to know more about the role of BAT in Japanese macaques, and how this interacts with thick winter fur in maintaining thermal balance.

Japanese macaques huddle more and sun themselves in open areas or in trees more in winter, obtaining 0.5–5°C total increase in skin temperature this way (Hanya et al. 2007), and also are known to enter and remain in hot springs (Hori et al. 1977). Huddling saves energy for individuals by reducing exposed body surface area, increasing ambient temperatures in the huddle, and, in time, allowing them to reduce heat production by physiological processes (Gilbert et al. 2010). Such low-cost behavioral and cultural strategies, especially huddling, seem likely ways for hominins to reduce individual heat loss and decrease heat production especially at night.

Young animals lose heat across a larger surface area and hence have more difficulty keeping warm despite winter fur (Jessen 2001: 148). Many large mammals give birth

to relatively large infants, in spring, which grow rapidly during the short temperate season (Jessen 2001). Japanese macaques show some relationship between latitude and seasonality of birth, which seems to be linked to poor nutrition in winter (Fooden and Aimi 2003). BAT may play a role in keeping both young macaques and newborn reindeer warm, but, in the latter case, is converted to white fat by two months old (Devlin 2015; Soppela et al. 1991). Huddling may be important in cool conditions for slower growing young primates, while also providing thermal benefits for mothers (Li et al. 2010; Ueno and Nakamichi 2016). The development of seasonal birth in hominins in middle latitudes (Mussi 2007) is unlikely because human reproductive demands are spread throughout the year as is environmental variability (Ellison 2008). Generating extra heat to keep warm is likely to have been more of a problem for hominin infants, with a pressing need to allocate energy to growth, than for adults (Mateos et al. 2014). The high growth costs of activation of BAT soon after birth would have been prohibitive in most conditions. Huddling is likely to have been a useful strategy with minimal trade-offs when at rest. On the move, carrying infants could provide the benefits of skin to skin contact, but the lack of a grasping toe and extra weight would have made grasping on to body hair less effective for hominin infants than for other young primates. Carrying infants substantially increases maternal energy expenditure (Wall-Scheffler et al. 2007), while using a carrying device reduces these by 16% and at the same time provides extra insulation.

In conclusion, a strategy based on warm winter fur and subcutaneous fat would have kept hominins warm enough and is plausible given the limited trade-offs. We need to know more about the timing and nature of changes in human body hair and subcutaneous fat deposits to assess how effective it would have been for lowering energy expended in heat production. BAT may have played a supplementary role for surviving in temperature extremes for adults and particularly infants. Vulnerability of infants to heat loss would have been a critical problem for hominins practicing this strategy, which could perhaps have been mitigated by a combination of huddling at night and use of a carrying device in the daytime.

HIBERNATION

Most hibernators are small mammals, but because body mass has a strong influence on the nature of cold adaptation, this discussion focuses on hibernating bears. These include the Middle Pleistocene bear species *Ursus deningeri*, as shown by the large number of bones in the cave site of Sima de los Huesos (Garcia and Arsuaga 2010). The body temperature at which hibernating mammals increase heat production to avoid freezing is relatively low, reducing energy costs (Jessen 2001: 143). Energy savings for bears as a result of hibernation (including reduced costs of activity as well as keeping warm) are estimated roughly as 30% over summer basal metabolic rate (Davenport 1992: 133–134). Bears tend to use natural shelters when these are available (Stiner 1998), and otherwise construct burrows or use oth-

er natural hollows such as those provided by the roots of fallen trees. Like simple human shelters, these create small pockets of circulating airflow retaining body heat, and reducing airflow over the body (Chu 2009). However, hibernation is most important, as far as bears are concerned, for surviving a shortfall in resources in the winter (specifically plant, insect, and small vertebrate foods); their thick fur, large body mass and cardiovascular physiology all make them well suited to cope with cold temperatures (Davenport 1992; Stiner 1998).

Female bears that are hibernators delay implantation until the denning season, and have flexible timing of birth (Friebe et al. 2014). Highly altricial bear cubs are born and suckled in the den and kept close to the mothers body during the hibernation period, providing protection from the cold, and are kept in the den during subsequent winters (Friebe et al. 2014). This is an energy intensive reproductive strategy reflected in low litter sizes and long interbirth intervals. The main cause of mortality in hibernating bears is starvation and this particularly affects cubs since adults can leave the den if their food supply runs out (Friebe et al. 2014). On one hand, hibernation would have helped to keep a small hominin infant warm in winter, reducing trade-offs between growth and heat production. On the other hand, for early European hominins, the loss of infants or young children due to starvation or predation during hibernation would be a severe cost.

An ability to obtain an adequate quantity of food beyond that needed for normal body maintenance in order to lay down adequate fat is particularly crucial for female reproduction (Lopez-Alfaro et al. 2013), with bears with less than 20% body weight made up of fat on entering hibernation not reproducing (Robbins et al. 2012). Brown bear females gain approximately 26kg to 62kg before winter in Europe (Swenson et al. 2007). The summer and autumn trade-offs between energy acquisition for insulation and winter sustenance as opposed to body maintenance, as well as trade-offs in time spent on foraging and other activities, would have been high, although concentrated in a time of year with richer resources. Construction of a den, where natural shelters were absent, would involve additional trade-offs in the allocation of time and energy.

Black and brown bears have distinctive metabolic and biochemical characteristics that allow them to maintain muscle, bone, and protein, and avoid the negative effects of limited kidney function during hibernation (Barboza et al. 1997; Seger et al. 2011; Stenvinkel et al. 2013). Humans could not survive even short periods of inactivity and anuria without fatal complications (Stenvinkel et al. 2013). Brown adipose tissue plays an important part in arousal from hibernation (Cannon and Nedergaard 2004). Some of the important characteristics associated with hibernation are based on changes in gene regulation, rather than functional genes, with expression in key organs changing during hibernation (Fedorov et al. 2011; Villanueva-Canas et al. 2014). Some bear species hibernate only in the northern part of their range, and are closely related to non-hibernating species. While no great ape species hibernate, a few

primate species do so in challenging tropical environments. The multiple cases of closely related hibernators and non-hibernators, and role of regulating genes, small changes in which can produce big phenotypic differences, makes it more likely that a similar adaptation could have arisen once in the hominin lineage.

Sleeping hominins would have been vulnerable to predation, especially since they lacked the strength, claws, and teeth of bears. Denning bears are relatively helpless and the secrecy of lairs is key to avoiding predation (Stiner 1998). A range of large carnivores (including bears) were using caves as hibernation, denning, and eating locations during the Middle Pleistocene, and would have posed a threat to hominins, as well as competing for suitable locations.

Overall, the primary benefits of hibernation for hominins would have been for keeping juveniles warm. Given the smaller body size and possibly thinner hair of hominin adults, winter energy savings would have been lower than for bears. A relatively high weight gain in summer and autumn would be required, and the risks of starvation for adults and juveniles would be higher. This seems an unlikely thermoregulation strategy for hominins.

PHYSIOLOGICAL HEAT PRODUCTION AND MUSCLE INSULATION

Stegmann and colleagues (2002: 579–580) proposed that Neandertals relied on ‘a substantial arsenal of cold protection mechanisms,’ including ‘a major, high-energy metabolic adaptation facilitated by modest amounts of highly thermogenic brown adipose tissue,’ combined with a number of behavioral and cultural defenses. Recent research has provided measurements of BAT in human adults, and documented the effect of repeated exposure to cold and contribution to heat production, with implications for the original hypothesis, which are discussed below. Without any form of insulation, hominins would have been at risk of hypothermia at the lower end of the estimated temperature range at most sites (see Table 3). While the earliest European fossils are too scanty to indicate whether their body form was warm or cold adapted (Carretero et al. 1999; Robson and Wood 2008), morphological adaptations are evident by 500 kya (Arsuaga et al. 1997, 2015; Stringer et al. 1998), supporting the argument that the occupants of Europe experienced selection in cool conditions before 400,000 years ago. If so, it may be worth considering the possibility that they could have stayed warm enough by means of such cold protection mechanisms, without any significant behavioral or cultural thermoregulatory behavior.

By 500 kya, early European hominins could have benefited from the insulation provided by muscle (Arsuaga et al. 2015). A thick muscle layer can provide as much as a 5% reduction in heat loss and this benefit can be deployed by learning to limit muscle activity (Glickman-Weiss et al. 1993; Stegmann et al. 2002; Stegmann 2007). This may be a factor in the cold tolerance shown by the ‘Iceman,’ Wim Hof, who regularly undertakes feats of endurance including short-term exposure to extreme cold (van Marken Lichtenbelt, personal communication). In addition, the habitual

activity levels associated with such thick muscle are important for keeping warm. Even in extremely cold conditions exercise can be enough to maintain core temperature (Toner and McArdle 1988; Young et al. 1996). However, estimates based on basic physical principles suggest that robust body proportions and increased musculature would not have prevented hypothermia when at rest (Table 4; Aiello and Wheeler 2003).

Recent studies have shown that BAT is present and active in human adults as well as newborns (reviewed in Devlin 2015), supporting the argument that this was so in other hominins. Further, mild cold acclimation increases detectable BAT volume and activity (van der Lans et al. 2013). The failure of a recent study to identify unusual levels of BAT activity in the ‘Iceman’ suggests to the researchers that BAT may be most important during extended periods of mild cold exposure (such as those experienced by the early occupants of north-west Europe) rather than short-term exposure to extreme cold (Vosselman et al. 2014). One of the key characteristics of BAT, making it valuable for hominins, according to Stegmann and colleagues (2002) is that a very small amount of BAT would have made a major difference in cold defense. However, based on current measurements of adult human BAT, and rodent data (taking scale differences into account), BAT may contribute only c. 2.7–5% to human basal metabolic rate (BMR), a figure that is consistent with estimates based on positron emission tomography (PET) scanning of glucose uptake in human BAT (van Marken Lichtenbelt and Schrauwen 2011). A variant of classical brown fat, ‘beige fat,’ identified in mice, has the capacity to switch between energy storage and energy dissipation (Wu et al. 2012). Beige fat is of interest here because it could mean that humans and perhaps also earlier hominins were capable of higher levels of heat production in cool conditions than is suggested by clinical measurements of BAT. The role and development of beige fat in human adults is an important area of future research (Devlin 2015).

Recent experiments carried out in the Netherlands showed that mild cold-induced thermogenesis (non-shivering thermogenesis or NST) increased by about 7% of RMR (resting metabolic rate) as a result of a relatively short period of acclimatization (ten days, 15–16°C, 6 hours per day) (van der Lans et al. 2013). This increase occurred in parallel with BAT activity, so this study provides evidence that BAT is responsible for increased heat production in response to exposure even to quite mild conditions. A winter increase has been observed in Dutch subjects from 7% to 11.5% of RMR (van Ooijen et al. 2004). In addition to improving comfort in cold conditions, NST is likely to increase the range of survivable temperatures because, if necessary, heat production can be even further increased by shivering (Cannon and Nedergaard 2004).

Studies of populations practicing traditional subsistence strategies in colder conditions indicate that heat production at higher levels for longer time periods is possible for humans. BMR increases with decreasing mean annual temperature, when body mass, sex, and age are controlled for (Froehle 2008; Roberts 1978). Studies of four Siberian

TABLE 4. ESTIMATED LOWER CRITICAL AND MINIMUM SUSTAINABLE TEMPERATURE*
(BM=body mass; BMR=basal metabolic rate, SA=surface area, LCT=lower critical temperature,
MST=minimum sustainable temperature SH=Sima de los Huesos).[†]

	BM	Stature	BMR	BMR	SA	LCT1**	MST1**	LCT2 ^{††}	MST2 ^{††}	LCT3 [°]	MST3 [°]	LCT4 ^{°°}	MST4 ^{°°}
	(kg)	(cm)	(w)	*15%	(m ²)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)
Neandertal	80.8	167	91.63	105.37	1.90	26.8	6.5	25.9	3.7	25.3	1.9	16.7	-23.9
<i>Homo sapiens</i>	70.0	177	82.28	94.62	1.86	27.7	9.1	26.8	6.5	26.3	4.9	18.4	-18.7
SH	76.1	170	87.60	100.74	1.87	27.1	7.4	26.2	4.7	25.7	3.0	17.3	-22.0
	BM	Stature	BMR	BMR	SA	LCT1**	MST1**	LCT2 ^{††}	MST2 ^{††}	LCT3 [°]	MST3 [°]	LCT4 ^{°°}	MST4 ^{°°}
	(kg)	(cm)	(w)	*25%	(m ²)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)
Neandertal	80.8	167	91.63	114.54	1.90	26.8	6.5	24.9	0.8	24.3	-1.1	14.9	-29.2
<i>Homo sapiens</i>	70.0	177	82.28	102.85	1.86	27.7	9.1	26.0	3.9	25.4	2.1	16.8	-23.6
SH	76.1	170	87.60	109.50	1.87	27.1	7.4	25.3	1.9	24.7	0.0	15.6	-27.2

*Following Aiello and Wheeler 2003.

[†]Body mass from Ruff (2010); stature from Carretero et al. (2012); all male.

**Estimates with muscle.

^{††}Estimates with elevated BMR.

[°]Estimates with elevated BMR and muscle.

^{°°}Estimates with elevated BMR, muscle and clothing.

populations gave BMR values on average 17.7% (f) and 15.2% (m) higher than expected (Leonard et al. 2002, 2005; Snodgrass et al. 2005), which are not related to any difference in diet (Leonard et al. 2005). In one of these populations, BMR increased by 6% in younger individuals in winter (Leonard et al. 2014), similar to levels documented in the Netherlands. Seasonal functional responses to cold could therefore result in a total BMR elevation of c. 21–23%. While BAT has not yet been studied in modern humans in cold climates, analyses of thyroid hormones provide support for the view that some of the high energy expenditure of circumpolar populations is in part a result of BAT thermogenesis (Devlin 2015). Recent clinical studies confirm that BAT activity is related to thyroid hormone levels (Broeders et al. 2016).

While these populations encountered very severe conditions: (Leonard et al. 2005), they also employed a range of highly effective technologies which would have buffered them from the cold. This evidence for long-term metabolic up-regulation may therefore be relevant to hominins with limited cultural insulation in milder conditions in north-west Europe. Metabolic up-regulation has the potential to increase the range of survivable temperatures, allowing individuals to physiologically sustain higher levels of heat production (Steegmann et al. 2002; Aiello and Wheeler 2003). However, the functional benefits of metabolic up-regulation, in terms of economic status, health, and reproduction, and links to survival rates and rates of hypothermia or injury, need to be addressed in order to demonstrate that this is a human cold adaptation (Steegmann 2007).

A range of costs for metabolic elevation can be iden-

tified (Snodgrass et al. 2007: 170–171). In an environment with limited food resources, the additional caloric demands of an elevated BMR increases dietary stress on populations in cold climates. Less energy available for growth and reproduction may lead to delayed fertility and slow growth. There may be both positive and negative effects on production of free radicals and implications for longevity (Snodgrass et al. 2007; Wallace 2006).

To what extent can a genetic basis for enhanced heat production mechanisms be identified in humans, highlighting possible changes that might have occurred as hominins adapted to cooler conditions in the past? A study of potentially functional variation in 28 genes directly related to BAT metabolism, or with a regulatory function for this, identified signals of selection (in East Asians) only in one gene, *LEPR* (Sazzini et al. 2014). Studies of cold adaptation in Siberian genetic data (snps) did not highlight *any* genes associated with BAT (Cardona et al. 2014; Clemente et al. 2014). However this is really only the beginning of research on the genetic basis of BAT as a cold adaptation; it is possible that variation in regulatory regions for these genes is key.

A possible additional solution to keeping warm is highlighted by a study of Wim Hof, the ‘Iceman,’ mentioned above, is the application of a specific breathing method which greatly increases the metabolic activity of the respiratory muscles (Vosselman et al. 2014). This may account for the capacity of this individual and his brother to produce heat at 40% above Resting Metabolic Rate (RMR) while most young adult males did so in the range 10–30%, and it would be interesting to see further larger studies of

this technique.

Infants and younger children are at great risk of thermal stress because of their small body size and higher thermoneutral zone (Mateos et al. 2014). Hypothermia is a major cause of morbidity and mortality in infants (Mance 2008). BAT has been identified in infants in the supraclavicular region, near the spine and axilla (Lidell et al. 2013; Rasmussen et al. 2013), in volume similar to that in adults (Virtanen et al. 2009). Early studies showed that even mild exposure to cold stress resulted in very high increases in heat production in infants to 71–121% above resting level (Dawkins and Scopes 1965; Lidell et al. 2013). There are no studies of BMR up-regulation in children in circumpolar populations. For human infants, there is a strong trade-off between energy expended in thermoregulation and in growth (Jessen 2001: 148). The strength of this trade-off would be affected by body size and growth rates in childhood (Mateos et al. 2014). While a capacity for intense heat production under stress would be valuable, it would also have been important to avoid such situations occurring too often. There may therefore be strong benefits to behavioral and cultural strategies including skin-to-skin contact with a parent, particularly at night, and use of insulative carrying devices (Leonard et al. 1994). Another interesting suggestion is that under conditions in which there was a high demand for energy for thermoregulation, selection for slower growth and smaller body size in childhood may have occurred (Mateos et al. 2014). Unfortunately, evidence for growth rates and body size in early childhood is currently lacking for the period in question.

A larger body mass at and following birth could have thermal advantages for infants. Body mass and height correlate with latitude in infants and children to the same degree as adults (Cowgill et al. 2012). The ACP1*A allele, highlighted by Steegman and colleagues (2002), is most frequent at high latitudes and gives rise to a growth enhancer. Supporting this, there is a stronger effect of season of birth on birth weight for infants in Italy with the ACP1BA phenotype, who also tended to be larger (Gloria-Bottini et al. 2009).

Calculations based on basic physical principles and estimates of skin surface area, thermal conductance, and the maximum sustainable elevation in BMR suggest that elevated BMR and thick muscle alone would have been adequate for survival for adults at some sites in north-west Europe in winter (see Table 4), if temperatures were towards the top of the estimated range (see Table 1). This is particularly the case if BMR elevation was high—at a level of 25%—which is conceivable based on observations of humans in the circumpolar region in winter. At other sites they would have been at risk of hypothermia, especially at night. Wet weather and wind could have posed further problems. More research is needed to establish the adaptive nature of enhanced heat production in humans, and assess whether cool conditions could have selected for this in earlier hominins. This strategy would have involved strong winter trade-offs between energy allocation to heat production and body maintenance, and time allocation to

foraging versus other activities. Finally, additional behavioral or cultural solutions were probably essential for babies. It seems that with this strategy hominins would have led a rather marginal, risky existence in north-west Europe.

SIMPLE CULTURAL INSULATION AND ENHANCED HEAT PRODUCTION

Is it more plausible that the early occupants of north-west Europe combined physiological adaptations including enhanced heat production with simple cultural strategies for keeping warm? Recent hunter-gatherer groups provide the most relevant evidence to address this question, although all also use fire. Steegmann et al. (2002) identified hunter-gatherer populations from Tierra del Fuego as a useful model for Neandertal biological and cultural cold adaptations, because of the wet, windy, cool weather conditions of that region and their relatively simple insulative technology. This discussion draws on ethnographic descriptions of hunter-gatherer groups with a mean temperature of the coldest month between 0°C and -10°C at the center of their distribution, according to Binford's (2001) database, putting the Tierra del Fuego populations in a broader context. I focused on groups included in the Electronic Human Relations Area Files World Cultures database. An emphasis on the ethnographic record also is useful because evidence for hominin use of clothing and shelter (and other cold-weather technologies) is limited before 400,000 years ago (Chu 2009; Gilligan 2010).

Clothing is an important source of insulation which increases with thickness primarily due to air trapped near skin by layers and/or animal fur (Gilligan 2010). For this discussion, it is important to distinguish between simple (or 'cape-like') and complex (or 'specialized cold-weather') clothing (Gilligan 2010; Collard et al. 2016). Draped, single-layered clothing can be manufactured in the absence of specialized hide working and sewing technology and exploitation of particular fur-bearing species, all of which is only evident in the record much later (Collard et al. 2016; Golovanova et al. 2010; Soressi et al. 2013). According to Gilligan (2010: 25), 'where the raw materials are animal hides, simple clothing requires little more than basic skin-preparation techniques, mainly cleaning and scraping, achieved most effectively with scraper tools of various descriptions' and possibly piercing implements. Hominins had the technology needed to make simple clothing before 400,000 years ago. Skin preparation is documented just after the study period at the site of Schöningen, Germany, based on residues and wear and manufacturing traces on stone tools, and cut-mark distribution (Rots et al. 2015; Voormolen 2008). The preservation at this site is exceptional, and the absence of similar evidence from older sites reflects the scarcity of such studies. It therefore seems reasonable to consider the possible role of clothing and related forms of cultural insulation in this period, and to look at the ethnographic evidence for information.

The ethnographic evidence confirms that quite simple clothing, providing less than the maximum insulation, was adequate for hunter-gatherers in these conditions. Sev-

TABLE 5. CHARACTERISTICS OF HUNTER-GATHERER WINTER CLOTHING.*

Name	MWT °C	Tailored	Layers	Shoe	Mittens	Hat	% Coverage	Skin Treatment
Ona	1	No	1	Yes	No	No	90/72.5	Yes
Yahgan	2	No	1	Yes	No	No	62/44.5	Yes
Ainu	-7	Yes	1 or 2	Yes	No	Yes	90	No
Alutiq	-4	Yes	2	Yes	Yes	Yes	99	No
Central Ojibwa	-8	Yes	2	Yes	Yes	Yes	100	Yes
Klamath	-3	Yes	1	Yes	Yes	Yes	17.5–100	No
Aleut	-10	Yes	2	Yes	Yes	Yes	100	No
Crow	-8	Yes	2	Yes	Yes	No	91/73.5	No

*Information derived from the Electronic Human Relations Area Files World Cultures database.

eral populations wore only one layer of clothing, which included animal fur in winter (Batchelor 1927: 55–56) (Table 5). Others wore two layers consisting, for example, of a skin undershirt worn under a long parka (Birket-Smith 1953: 64). Fur was a key material for clothing for most of the populations discussed here, but vegetable fiber, skin, broadcloth, fishskin, and intestines also were used (Batchelor 1927: 55–56; Birket-Smith 1953: 64; Densmore 1929: 30; Ohnuki-Tierney 1974: 20; Spier 1930: 207). Most of the garments worn in the case studies were somewhat fitted and shaped, reducing heat loss by minimizing air movement (Gilligan 2010), but only the Alutiq are described as wearing shaped, sewn clothing with both sleeves and legs (Birket-Smith 1953: 64–66). The main Ona and Yahgan garment consisted of a loose fur cape. In most cases, clothing covered three quarters to 100% of the body (see Table 5), following Wales's (2012) classification. By contrast, the Yahgan fur cape reached only to the waist, although it was sometimes combined with moccasins and leggings which covered the calves (Cooper 1946: 86; Gusinde and Schütze 1937: 53, 56). A wet climate that spoils clothes and the availability of natural shelter may explain the smaller size of clothing in this population (Gilligan 2010; Gusinde and Schütze 1937: 51). The total area of the body covered by clothing is more important than the presence or absence of specific items. Relatively little heat is lost from the head (Vreeman and Carroll 2008), and the extremities in general (Steegmann 2007), but footwear may be important for combating frostbite. Some form of footwear was available in each case although not always worn (Birket-Smith 1953: 67), and shoes were often stuffed to increase insulation (Birket-Smith 1953; Ohnuki-Tierney 1974).

According to Gilligan, draped, simple clothes with one layer only offer one to two clo of thermal protection (Churchill 2014; Gilligan 2010); a simple cloak of animal fur covering most of the body is likely to have provided slightly less than the 1.94 clo given by the fur of temperate latitude mammals (Cena and Clark 1978; Churchill 2014). However even one clo can reduce heat loss by about 44% (Aiello and Wheeler 2003). Such simple clothing would

have largely removed the risk of hypothermia for hominins under average winter conditions, although they would still have needed some extra energy to keep warm (see Table 3: calculations are equivalent for thin body hair and light clothing). As Gilligan (2017) points out, clothing is likely to have been particularly important because, without it, hominins could not survive outside physiological thresholds in the open where they were exposed to wind. On the other hand, the benefits of clothing are substantially reduced in high winds and wet clothing increases heat loss (Churchill 2014). Ona men sometimes removed and folded cloaks to keep them dry (Gusinde 1931: 296). Waterproof clothing is present in a few cases, for example, hooded rain parkas sewn from strips of intestine and bird skin with feathers outwards (Birket-Smith 1953: 64–65), but is difficult to produce. Nevertheless the water-resistant qualities of some animal furs are stressed by commentators. It is possible that hominins would have had problems keeping warm enough in cool conditions when clothed if it was also often wet. Simple clothing would in addition have added to the energetic costs of locomotion (Churchill 2014: 154).

A review of the production process for simple clothes can provide further insights into trade-offs. A similar production process for clothes was employed by both Tierra del Fuego populations (Gusinde 1931: 302; Gusinde and Schütze 1937: 68–74). Skins were removed after hunting (Gusinde 1931: 387; Gusinde and Schütze 1937: 68); two guanaco skins were used for Ona cloaks (Gusinde 1931: 302). Making clothing was women's work and would trade-off with time spent in other activities, which for Yahgan women included fishing for certain resources which only they could obtain (Chapman 1982: 42–44). The skins were stretched on a framework of sticks, cleaned with a scraper, kneaded all over to soften the hide, and greased with a mixture of ochre and fat (in the case of the Ona). Both cleaning and softening were physically tiring. The drying process took several days. When sewing together two pieces, a woman placed the edges next to each other, pierced both with a fine awl and then pushed through a tendon fiber by hand (Gusinde 1931: 302). Sandals or moccasins had a similarly simple

construction, involving cutting a piece of leather to measure from the guanaco's leg, folding the thinner end over the top of the foot, cutting holes, and drawing the whole together with a small thong (Gusinde 1931: 304).

Animal fat could be smeared on the body to protect the skin from wind, cold, and snow, and to cope with cold (Chapman 1982: 32; Gusinde 1931: 298). The Ona applied animal fat almost daily (Chapman 1982: 32), while the Yahgan used a similar coating even more extensively (Gusinde and Schütze 1937: 51), and central Ojibwa men coated their faces in a strong wind. The Ona used a shoulder blade of guanaco or seal for melting fat or extracting grease, the Yahgan a large shell (Cooper 1946). This was mixed with heated or roasted ochre, and other substances such as charcoal (Chapman 1982). This fat layer probably provided a similar amount of insulation to the equivalent thickness of subcutaneous fat, less than light clothing, but may have played an important role in reducing wind chill. For the Ona, this coating also had roles in ceremony and hunting. This fat was a scarce resource—guanaco are comparatively lean ungulates (De Nigris and Goñalons 2005; Speth and Spielmann 1983), although marine mammals (the source of fat used by the Yahgan) are much fatter.

Winter shelter was often slightly subterranean, with a wooden frame draped with various covers and insulating materials, more or less enclosed, and with varying degrees of floor cover. For example, the Ona constructed a windbreak, or a conical hut when wood was abundant (Chapman 1982: 26–28; Gusinde 1931: 277–282). Both were made from a frame of wooden poles and a large leather cover, built facing away from the prevailing wind. The ground was hollowed out and earth piled on the bottom edge of the cover, and brush, leaves, lichen, and moss were strewn on the ground (*ibid.*). Windbreaks create pockets of circulating airflow in which heat generated by bodies or fire is retained, and, more importantly, cut down wind chill (Chu 2009; Wilkins 2007). Even smaller structures could be useful. Ojibwa winter travelers who needed to spend a night outdoors would construct a snowbank on the windward side and sleep between the fire and bank, or light a fire and sleep on the warm spot afterwards (Densmore 1929: 143). The larger size and more solid materials used for structures by some of the hunter-gatherer populations can be explained by greater permanence of their winter settlements (Binford 1990).

The leather cover for a shelter was constructed from 8 to 16 firmly sewn animal skins (Gusinde 1931: 282). Leather was prepared by the method described for clothing, with the addition that the hair was scraped off, and the cover was particularly thickly greased on both sides. It lasted a couple of years. Women carried the leather cover, and, where trees were scarce, 8 to 12 poles, a load that would have substantially added to the energy used while walking to a new place of residence (Gusinde 1931: 282). Erecting the Ona hut took less than an hour for a man and woman (Gusinde 1931: 277).

Within the shelter, bedding or nightwear, particularly of animal skins, was used by these hunter-gatherer pop-

ulations, and people often huddled together, especially children. Cloaks doubled up as bedding material (Bridges 1949: 368; Gusinde and Schütze 1937: 54). Bedding and clothing are calculated to have a much stronger effect on heat losses by radiation, conduction, and convection from the surface area of a sleeping hominin than shelter or fire (Sørensen 2009), and huddling would have further warmed the ambient temperature of air next to the skin.

As discussed above, human infants are vulnerable to hypothermia. Newborn Ona infants were placed in a leather sack lined with soft furs, down feathers, and tufts of wool (Gusinde 1931: 530). A mother secured her baby next to her skin on her back within her cloak using a leather strap when traveling (Gusinde 1931: 534); and, slept next to the baby to keep it warm at night. Yahgan women would sometimes enlarge their capes so the children could shelter underneath while traveling (Gusinde and Schütze 1937: 59). Babies often were placed in a cradleboard or other carrier, lined with dried moss, small furs, and mats, for transport (Hilger 1951: 14; Pearsall 1950: 340; Rogers 1962: 37), which was sometimes also placed next to the mother at night (Ohnuki-Tierney 1974: 56).

Some groups moved to locations within their territory in which climate was milder in winter. For example, the Klamath occupied large fixed winter residences, in a sheltered sunny spot near running water or a hot spring that would not freeze (Spier 1930: 10). Coastal locations can also have favorable microclimates (Cohen et al. 2012).

The trade-offs in terms of time and energy spent in production versus other subsistence activities, raw materials, and transport costs would have been higher for the early occupants of Europe than recent hunter-gatherers in a number of ways. Lacking current efficient subsistence tools, hominin foraging probably took more time, making trade-offs with other activities more important than for recent hunter-gatherers, especially on short winter days. However, dividing production and foraging activities among the group could have helped to limit trade-offs. If hominins already had relatively high transport costs, for example, due to large body mass or less efficient locomotion, this has important behavioral implications (Verpoorte 2006; but see Heyes and MacDonald 2015). These include a more significant trade-off with foraging efficiency when drying hides or using a shelter in the same place for several days, with daily foraging costs increasing faster as resources are used up and it becomes necessary to walk further. Because the benefits of shelter pay off over the duration of occupation, if hominins needed to move residence frequently, they are likely to have built ephemeral structures, if any (Verpoorte 2006). While investment in transportable shelters might be worthwhile, without alternative means of moving these about this would have to be balanced against already high energetic costs for walking. However, until body mass estimates are improved, it is difficult to argue that the early occupants of Europe faced higher trade-offs for using clothing and shelter than recent hunter-gatherers based on transport and movement costs (Heyes and MacDonald 2015).

In the preceding section, I discussed the possible relevance of enhanced metabolic heat production for hominins coping with cold in north-west Europe. This could have played a role in combination with cultural insulation strategies, particularly given that there is a small amount of evidence for use of enhanced heat production by recent hunter-gatherer populations living in similar conditions. One relevant study involved a small group of Kawésqar men ($n=9$) from Chilean Tierra del Fuego (Hammel 1960); this population occupied the western islands just to the north of the Yahgan, where the mean temperature of the coldest month is -0.3°C . In a night in which they were exposed to moderate cold, the drop in their RMR and internal body temperature was small, from around 37°C to 36°C . Steegmann et al. (2002) estimate that these men consumed c. 750kcal of energy during the night (about 20% of likely daily energy intake based on other active foragers).

A combination of simple clothing and elevated BMR would have protected against hypothermia in all conditions to which hominins were exposed and reduced the amount of extra heat production required, although persistent rainfall could have been a problem. Clothing would have been crucial for protection on the move. Clothing that covered infants, and insulated carriers, were necessary for protecting infants from hypothermia. At night, bedding and huddling would have been relatively low-cost strategies which strongly reduced energy expenditure. The trade-offs involved seem plausible for hominins, but we really need to know more about transport costs. Shelter carries additional benefits, with somewhat higher costs; this would have perhaps become more important when hominins faced colder conditions and stronger winds after 400,000 years ago.

DISCUSSION

In conclusion, two strategies for keeping warm in the absence of fire are plausible for the early occupants of north-west Europe—winter fur and fat, or cultural insulation combined with biological heat production. These strategies would have avoided any risk of hypothermia in winter in the conditions in which generally hominins lived, although they would have used some additional energy to keep warm. In these conditions the trade-offs in summer and winter would not have been severe. Because of the additional energetic demands of growing, an extra means of keeping infants warm would have been important. Baby wraps or carriers provide a possible solution when on the move; the costs would have been lower for production in combination with clothing, providing a possible argument in favor of the second strategy.

Seasonal migration to areas with milder winters would change the conditions experienced by hominins and the strategies they employed to keep warm; the impact depends both on the distance hominins could migrate, and the climate gradients at the time. There is no archaeological evidence for long distance movement by the early occupants of Europe. The maximum distances between the source area of a rock and locations at which artifacts made out of these stones were deposited in archaeological sites

tend to be short (tens of kilometers) (Feblot-Augustins 1997; Gamble and Steele 1999). A number of factors, including the need to keep pace with slower children, pregnant women, and older adults, and foraging in unfamiliar areas on the way, are likely to have restricted the distances that could be traveled during a day (Hosfield 2016; Kelly 2013; Rockman 2003; Wall-Scheffler 2012). It seems unlikely that hominins would have travelled further than 20–30km in a day, the furthest distance hunter-gatherers comfortably walk while foraging in a range of terrain (Kelly 2013). Based on current temperature gradients, seasonal migration westwards along the northern French coast, taking perhaps twenty days at a daily travel distance of 20km, would have brought hominins to areas with winter temperatures about four degrees warmer than listed in Table 1 and might have allowed them to avoid freezing temperatures. River and coastal routes would have had a number of benefits for migration (Cohen et al. 2012). Based on air temperature, in this scenario hominins would have been able to avoid hypothermia solely based on physiological defenses—a thick layer of muscle and up-regulated BMR. However, they also would have encountered more rain on the coast, which would have added to heat loss from the body. This scenario makes quite a difference to my conclusions and the evidence for seasonal migration requires more investigation.

Producing additional heat has high energy costs, which in an environment with limited resources would trade-off with energy needed for growth and reproduction for hominins. These costs would be highest in cold periods of the year, when the availability of plant foods is lower and the fat content of wild large game may decrease to two to three percent (Speth and Spielmann 1983). This presents the most problems for a very energy-expensive strategy based primarily on enhanced heat production, but is also relevant to the strategies involving fur or clothing insulation. Ways of obtaining adequate carbohydrates or fat in winter, include targeting resources with high fat content (bears, beavers, fish, waterfowl), storing fat, and targeting winter underground storage organs (Hosfield 2016; Speth and Spielmann 1983). Some fat-rich species were present in north-west Europe in winter (Hosfield 2016), and suitable resources may have been available in winter in waterside environments (Cohen et al. 2012). An ability to actively hunt or fish would have aided procurement of animal food, targeting fat-rich individuals; hominins were clearly capable of the former by 300,000 years ago (Voormolen 2008). An additional issue is that uncooked meat and fish is very demanding to chew (Carmody and Wrangham 2009). As discussed above, fermentation could have helped to soften such foods and increased energy intake as well as aiding preservation (Speth 2017). In developing hypotheses about survival with limited use of fire we need to consider connections between different domains of behavior.

Sandgathe and colleagues (2011) argue that Neandertals were opportunistic users of fire, raising questions about how Neandertals coped in cold phases, as the authors point out (Dibble et al. 2017). In the late Middle and

Late Pleistocene, Neandertals were present in colder conditions than those endured by their ancestors. For example, winter air temperature reconstructions from UK sites attributed to Marine Isotope Stage 3 range between approximately -3°C and -27°C (Coope 2002). While these authors stress Neandertal cold-adapted morphology, a key element of this morphology, an increasingly barrel-shaped torso, probably had limited benefits in terms of preventing heat loss (Aiello and Wheeler 2003; see Tables 3 and 4). As can be seen in Table 3, this would have made a strategy based on not terribly dense fur and fat impossible, while high levels of heat production combined with simple clothing would have allowed adults to avoid hypothermia. However, energy demands from food would have been extremely high, particularly in the phases in which, according to Sandgathe and colleagues, fire was rarely if ever used. As Dibble et al. (2017) point out, if Neandertals were not cooking, they would also have needed to obtain more calories than fire-using humans in similar conditions. Further attention to Neandertal fire-free survival strategies is needed to back up the late chronology.

The arguments presented above depend on estimates of winter temperatures from hominin sites, and on estimates of minimum sustainable temperatures for hominins, neither of which are likely to be exactly right. This approach allows comparison, for example, indicating that a strategy based primarily on physiological heat production put hominins at greater risk of hypothermia in cool conditions than fur and fat. It is most likely that winter temperatures are underestimated; in addition, the extent to which wind chill and rain are taken into account is limited. This will not necessarily change the conclusions, as the minimum sustainable temperatures associated with clothing and fur are several degrees lower than those reconstructed at any hominin sites. Gilligan (2007) suggests a lower minimum sustainable temperature value for acclimated, unclothed humans than the estimate provided by Aiello and Wheeler (2003). However, these estimates are not equivalent—Gilligan's estimate is for humans with some cultural means of keeping warm, and some acclimation, while Aiello and Wheeler's is for an average, not acclimated human; the estimates for hominins are therefore probably not too high. Finally, assessment of the plausibility of strategies for hominins in the light of trade-offs is qualitative. In the future, improved understanding of hominin energy and time budgets might improve our ability to understand different allocation of limited resources by hominin species, but we are currently a long way from having all the information needed to apply such approaches (Heyes and MacDonald 2015; Verpoorte 2006).

FUTURE RESEARCH

The availability of ancient DNA from Neandertals, Denisovans, and early *Homo sapiens* makes it possible to clarify when some human adaptations emerged, and could also highlight distinctive adaptations of these hominins and their common ancestors, such as winter fur. Nuclear DNA from fossils dating to the period under discussion may

yield information about adaptations in the future (Meyer et al. 2016). While some polymorphisms in a gene associated with hair variation may have been the focus of selection in human evolution (Abbasi 2011), multiple genes are likely to have been involved. Proboscidean genetics could provide insights into the evolution of hair cover for comparison with hominins (Roca et al. 2009). A study of a number of genes associated with hair characteristics, including length, did not establish any differences which might produce contrasting effects in proteins in *Mamuthus primigenius* compared with modern elephants (Roca et al. 2009); the authors suggest that 'future candidate genes will likely reside among the keratin and keratin-associated protein (KRTAP) genes'. A specific substitution in TRPV3 in woolly mammoths, which is absent in elephants, may have functioned in increasing hair growth, among other cold-related characteristics (Lynch et al. 2015). In addition, comparative studies of human hair follicle density in the context of other primates would help us to estimate the insulation afforded by winter fur for hominins.

A search at older sites for traces of hide-processing, similar to those recovered at Schöningen, would make a valuable contribution to assessing the likelihood of manufacture of clothes and bedding (Rots et al. 2015; Voormolen 2008). Understanding of hominin exploitation of small game and waterfowl, which include fat-rich species, and aquatic resources, in the European Lower Paleolithic has been restricted partly by limited research effort and requires continued attention. Recent research has highlighted a range of plant resources that are likely to have been available, in the winter as well as summer (Bigga et al. 2015; Hardy 2010); future research should target evidence for hominin exploitation of these plant resources. Experimental data on the insulation provided by simple clothing, an external fat layer, insulating baby carriers, and bedding would be useful for assessing the importance of these cultural strategies.

We need to know more about the evolution, mechanisms and genetics of human metabolic up-regulation, to understand the likely role in earlier hominins. Medical studies of NST focus on comfort rather than tolerance, and biological anthropology studies of metabolic up-regulation do not yet address fitness effects (Steegmann 2007), leaving us with limited knowledge of human *tolerance* of cold. Tracing BAT expenditure in the field is a challenging but developing area of research which could aid our understanding of the role in BMR upregulation (Devlin 2015) and support genetic studies. An existing study using ancient DNA to study cold adaptations showed very limited overlap between BAT-derived alleles identified in human populations and those in Neandertals and Denisovans, suggesting different mechanisms of cold adaptation (Devlin 2015; Sazzini et al. 2014). However, future research on human BAT should address possible regulatory differences (Jac Aarts, personal communication). A possible influence of BAT on bone mass may provide another way of assessing the role in hominins (Devlin 2015). While the research areas highlighted in this discussion range far from traces of

fire, it is hoped that a better understanding of how the early occupants of Europe coped with cold will help to resolve the chronology and illuminate the impact of fire use.

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